

Are soil lichen communities structured by biotic interactions? A null model analysis

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Abstract

Question: Are soil lichen communities structured by biotic interactions?

Location: Gypsum outcrops located next to Belmonte del Tajo, central Spain.

Methods: We sampled a total of 68 (50 cm × 50 cm) plots in gypsum outcrops from central Spain. Each plot was divided into 100 (5 cm × 5 cm) sampling quadrats, and the presence of all lichen species in every quadrat was recorded (6800 quadrats in total). We used two realistic null models to generate random communities unstructured by biotic interactions, and used them to test the hypothesis that soil lichen species co-occur less often than expected by chance.

Results: We found fewer species combinations and less co-occurrence than expected by chance. However, the latter result was dependent on the null model selected. The number of checkerboard pairs did not differ significantly from the null expectation.

Conclusions: Overall, our results suggest that gypsiferous soil lichen communities are structured by competitive interactions. They are consistent with studies conducted with a wide variety of taxa, and fill a gap in our knowledge of the factors driving the small-scale distribution of these important organisms.

Keywords: Biological soil crust; Community assembly rule; Null model analysis; Semi-arid; Species co-occurrence.

Nomenclature: Tutin et al. (1964–1980) for vascular plants; Hladun & Llimona (2002–2007) and Breuss (1996) for lichens.

Abbreviations: BSC = Biological soil crust; SES = Standardized effect size.

Introduction

The structure of biotic communities has important implications for ecosystem functioning and stability (Pimm 1984; Wilsey & Potvin 2000; Maestre et al. 2005a). Thus, it is not surprising that an important part of ecological research has been devoted to understanding how communities are structured and to developing general assembly rules to describe this structure (Diamond 1975; Connor & Simberloff 1979; Weiher & Keddy 1999). Among those developed so far, Diamond's (1975) assembly rules model, which predicts that species should co-occur less often than expected by chance because of competitive interactions, has been one of the most influential and hotly debated (Gotelli 2000). Even if facilitation has been found to be a prevalent force shaping the structure of communities in a wide variety of environments (Castellanos et al. 1994; Armas & Pugnaire 2005; van de Koppel et al. 2006), results of recent studies suggest that Diamond's (1975) predictions hold for most natural plant communities and non-parasitic animals (Gotelli & McCabe 2002; Gotelli & Rohde 2002).

Surprisingly, assembly rules have seldom been employed to describe co-occurrence patterns in moss and lichen communities (Wilson et al. 1995). Such communities are key biotic components of a wide range of ecosystems, including cold and hot deserts, boreal forests and the arctic tundra (Hahn et al. 1996; Belnap & Lange 2001; Nilsson & Wardle 2005). Several authors have suggested that, contrary to Diamond's (1975) predictions, these communities are not structured by biotic interactions such as competition (Watson 1980; Slack 1990; but see Wilson et al. 1995). We used null model analyses (Gotelli 2000) to test for patterns of co-occurrence of lichens forming biological soil crusts (BSC). Soil lichens are an important constituent of BSC in arid and semi-arid environments throughout the globe, and usually represent a later stage in its development (Lange et al. 1997). These organisms exert a great influence on ecosystem functioning by affecting nutrient cycling, soil

stability and infiltration (Evans & Ehleringer 1993; Belnap & Gillete 1998; Maestre et al. 2002), by influencing the establishment and performance of vascular plants (Eckert et al. 1986; DeFalco et al. 2001; Escudero et al. 2007), and by serving as habitat for a large number of arthropods and micro-organisms (Belnap 2001; Shepherd et al. 2002). Despite their importance, null models and assembly rules have not previously been used to evaluate co-occurrence patterns in BSC forming lichens. The main objective of this study was to test the hypothesis that these organisms co-occur less often than expected by chance (Diamond 1975), and thus are likely to be structured by competition. The role of competition for space as a main driver of community structure has been largely recognized in saxicolous lichen communities (e.g. Pentecost 1980; John 1989) and we predict that a similar result may be expected in BSC forming lichen communities because of their morphology, growth habit and substrate requirements (Belnap & Lange 2001).

Material and Methods

Study area and sampling

The study was conducted in gypsum outcrops near Belmonte del Tajo, central Spain (40°7'3" N, 3°18'30" W, 686 m a.s.l.; 8° slope; 220° SW aspect). The climate is mediterranean semi-arid, with a mean annual temperature of 14 °C and mean annual rainfall of 452 mm. The outcrops are surrounded by a well developed forest of *Quercus ilex* and *Pinus halepensis* (App. 1), but perennial plant cover within them remains below 20%. It is patchily distributed and dominated by species such as *Stipa tenacissima*, *Helianthemum squamatum* and *Lepidium subulatum*.

A total of 68 plots (50 cm × 50 cm), spreading over a homogeneous area of 1.3ha, were placed non-randomly on bare ground areas with well developed BSC located in the spaces between perennial plants (App. 1). In order to minimize the variability associated with small-scale differences in topography and to capture the greatest possible contrast in lichen community composition and structure, these plots were placed non-randomly in areas with well developed BSC (Bowker et al. 2002; Maestre et al. 2005a). However, a minimum separation distance between plots of 0.7 m was ensured to minimize the risk of sampling non-independent areas due to the spatial structure of BSC. Much of the spatial variation in the cover of BSC organisms in semi-arid mediterranean areas occurs at spatial scales smaller than the 50 cm × 50 cm quadrats used (Maestre 2003), and with this separation distance we aimed to remove potential sources of non-independence between sampling quadrats. Each plot was divided into 100 (5 cm × 5 cm) sampling quadrats,

and the presence of all lichen species in every quadrat was recorded (6800 quadrats). None of the sampling quadrats was fully covered by thalli of a single species (App. 2). Therefore, we believe that the scale used is appropriate to meet the objectives of the study (Maestre et al. 2005b). We focused only on lichens because they are the dominant component of BSC in gypsum outcrops of our study area (the cover of mosses is usually below 1%; Martínez et al. 2006). For each plot, the data were organized as a presence-absence matrix, where each row and column represents a different species and sampling quadrat, respectively.

Quantification of community structure

We used three indices to quantify patterns of lichen community structure: the number of species pairs forming checkerboard distributions, the C-score and the number of species combinations (see Gotelli 2000 for details on the statistical properties of these indices and on their performance in null model analyses). The first index is calculated by counting the number of unique pairs of species that never co-occur. The C-score is calculated for each pair of species as $(R_i - S)(R_j - S)$, where R_i and R_j are the matrix row totals for species i and j , and S is the number of squares in which both species occur; this score is then averaged over all possible pairs of species in the matrix. The number of species combinations was counted by checking the columns of each matrix for distinct arrangements. If a community is structured by competitive interactions, there should be more checkerboard species pairs than expected by chance, the C-score should be significantly larger than expected by chance and the number of species combinations will be smaller than expected by chance (Diamond 1975; Gotelli 2000; Gotelli & McCabe 2002).

The indices obtained from each matrix were compared with those derived from 10 000 randomly assembled 'null' matrices. Their statistical significance was calculated as the frequency of simulated matrices that had indices that were equal to or more extreme to them (Manly 1995). We used two null models for each comparison: (1) fixed-fixed and (2) fixed-equiprobable (Gotelli 2000). In both cases, species frequencies are retained in random matrices (i.e. rare species remain rare and common species remain common). The fixed-fixed method also keeps constant the number of species in each sample unit, while the fixed-equiprobable method allows any number of species from zero to the total number of species encountered. The performance of both null models with the indices employed has been extensively tested and both have good statistical properties (low Type I error and good power to detect nonrandomness; Gotelli & Entsminger 2003). They also share two characteristics that make them appropriate for the objective of this study (Gotelli 2000): (1) they

maintain the observed species occurrence frequencies, a conceptually satisfying assumption corresponding to a colonization model in which species colonize a given plot randomly with respect to one another and (2) the species occurrences are random with respect to one another, which is an appropriate null model for detecting patterns caused by species interactions.

We created null matrices with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 (see Gotelli & Entsminger 2006 for details). Although some aspects of this algorithm have been criticized (Sanderson et al. 1998), extensive simulation analyses have shown that it is statistically appropriate (Gotelli & Entsminger 2003).

Statistical analyses

To facilitate comparison with previous studies, a standardized effect size (SES) was calculated for each matrix as $(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$, where I_{obs} is the observed value of a given index of lichen community structure and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of the index obtained from the 10000 null communities (Gotelli & McCabe 2002). A one-sample t -test was used to test the null hypothesis that the mean SES measured for the 68 presence-absence matrices did not differ from zero (Gotelli & Rohde 2002). We performed six such tests (three indices \times two null models), so we used the Bonferroni procedure to correct the individual tail probabilities of these tests. Null model analyses and t -tests were conducted with Ecosim 7.22 (Gotelli & Entsminger 2006) and SPSS 13.0 (SPSS Inc. Chicago, IL) respectively.

Results and Discussion

The SES of the number of species pairs forming checkerboard distributions did not differ significantly from 0 when using the fixed-fixed null model (Fig. 1A, Table 1). With the fixed-equiprobable null model, the corresponding SES was lower than expected, although the effect was not significant after Bonferroni correction (Table 1). The mean SES obtained with the C-score was greater than 0 for both null models employed, but this departure was significant only for the fixed-fixed algorithm (Fig. 1B, Table 1). For both null models employed, the mean SES of the number of species combinations was significantly lower than 0 (Fig. 1C, Table 1).

According to our working hypothesis, we found evidence that BSC forming lichen communities were mainly structured by competitive interactions. The underlying rationale of this hypothesis was based on the widespread evidence of competition in lichen communities, and on

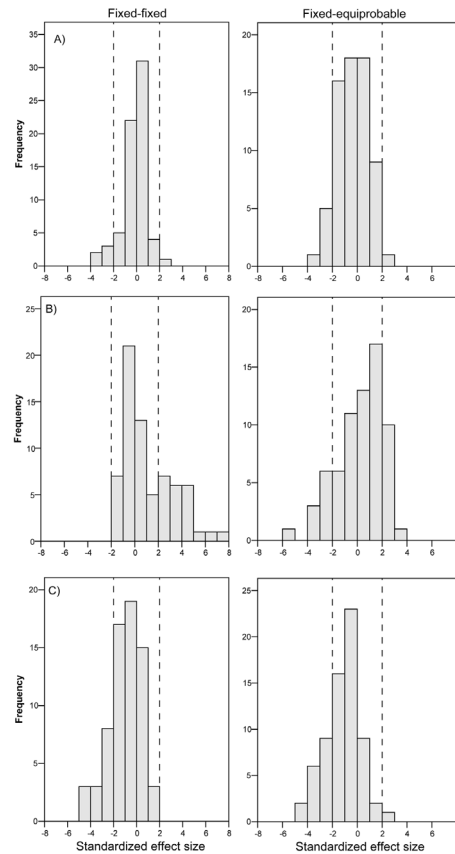


Fig. 1. Frequency histograms for standardized effect sizes measured in biological soil crusts presence-absence matrices. **A.** Number of species pairs forming checkerboard distributions; **B.** C-score; **C.** Number of species combinations. The null hypothesis is that the mean effect size equals 0. Dotted lines indicate 95% confidence intervals for this hypothesis.

the morphological and ecological characteristics of the lichens studied, which probably share the same niche requirements (Martínez et al. 2006). The clearest pattern that emerged from our analyses was that there were fewer species combinations than expected by chance. In addition, results from the C-score when using the fixed-fixed algorithm showed that soil lichens tended to co-occur less often than expected by chance. These results are in agreement with Diamond's (1975) assembly rules model and indicate that competition is the driving biotic force structuring soil lichen communities. In contrast, when empty sampling squares were included in the analyses (fixed-equiprobable model), we found a trend towards finding fewer checkerboard distributions than expected by chance, a result suggesting that facilitation, and not competition, is prevalent in the studied communities. It must be noted, however, that the effect size of this statistic

Table 1. Summary of null model analyses of biological soil crusts matrices. Significant *P*-values (after Bonferroni correction for multiple testing) are in bold.

Index	Null model	Average SES (unitless)	<i>t</i>	<i>P</i>
Checkerboard*	Fixed-fixed	-0.22	-1.67	0.101
Checkerboard*	Fixed-equiprobable	-0.34	-2.19	0.032
C-score	Fixed-fixed	1.16	4.46	< 0.001
C-score	Fixed-equiprobable	0.27	1.20	0.235
Number of species combinations	Fixed-fixed	-1.03	-6.22	< 0.001
Number of species combinations	Fixed-equiprobable	-1.16	-6.81	< 0.001

* Number of species pairs forming checkerboard distributions.

was small and non-significant after Bonferroni correction. Therefore, it is likely ecologically unimportant compared to the results in the other tests (number of species combinations and C-score from the fixed-fixed null model).

It has been argued that the presence of fewer species combinations than expected by chance not only arises as a result of competitive interactions, but can also be generated if the species differ in their affinities for non-overlapping habitats or in their potential for colonizing available habitats within the area studied (Pielou & Pielou 1968; Gotelli & McCabe 2002). Our observational approach does not allow us to distinguish between these hypotheses. However, we believe that differences in habitat suitability between plots and in colonization potential between the species studied are unlikely to explain our results because of three major reasons: (1) the relatively small dimensions of our study area; (2) the dispersal mode of the species found – through spores in most cases (App. 3; Clauzade & Roux 1985) and (3) the fact that all the species are common in well preserved gypsiferous outcrops from the Iberian Peninsula (Crespo 1973; Martínez et al. 2006). Further evidence is provided by the lack of relationship between the roughness of the soil surface, an important factor in determining small-scale differences in BSC composition (Bowker et al. 2006), and the number of species present in each plot (see App. 4). Thus, we believe that competitive interactions, rather than differences in habitat suitability between plots, were the main drivers of our results.

Our findings are consistent with widespread evidence showing interspecific competition among lichen species for space and nutrients (e.g. Armstrong 1991; Stone 1989; Shimizu 2004), and with studies emphasizing the importance of this biotic interaction as a driver of the structure of lichen communities developed over hard substrates (Pentecost 1980; John 1989). They also agree with Wilson et al. (1995), who found that competitive interactions were a key driver of the structure of soil bryophyte communities in New Zealand lawns, and with the results from a recent synthesis of presence-absence matrices from a wide variety of taxa, which suggest that observed co-occurrence in most natural communities was less than expected by chance (Gotelli & McCabe 2002).

The magnitude of the SES obtained varied with the choice of the co-occurrence index and type of null model. Similar results have been found in studies using different indices of community structure and/or null models to analyse the same data set (Gotelli & Rohde 2002; Gotelli & Ellison 2002; Tirado & Pugnaire 2005; see also Gotelli 2000 for a thorough discussion on the effect of null model type and index on the outcome of co-occurrence analyses). In addition to the suitability of the null models selected in our study, it must be highlighted that they have often been used with a wide variety of taxa (e.g. Connor & Simberloff 1979; Winemiller & Pianka 1990; Gotelli & Rohde 2002; Gotelli & McCabe 2002) and that the use of multiple, but conceptually and statistically plausible, null models has been recommended when evaluating co-occurrence patterns with presence-absence matrices (Gotelli 2000).

Our results represent, to our knowledge, the first empirical evidence of non-random species co-occurrence in BSC forming lichen communities. They fill a gap in our knowledge of the ecology of these important organisms and add to available evidence of the dominance of non-random patterns in natural communities (Gotelli & McCabe 2002). It has been recently shown that attributes of BSC, such as diversity and spatial pattern, directly influence ecosystem functioning in gypsiferous semi-arid environments (Maestre et al. 2005a). However, the influence of the documented co-occurrence patterns on key functional processes affected by soil lichens, such as nutrient cycling, remains virtually unknown. Facilitative/competitive processes among BSC components can be potentially relevant for ecosystem functioning if, for instance, they promote changes in the performance and dominance of N-fixing species such as *Collema* spp. (Davidson et al. 2002). Future studies focusing on how abiotic factors such as soil nutrients and microclimate modify observed co-occurrence patterns among soil lichens, as well as on the consequences of these patterns for processes such as nitrogen fixation and nutrient cycling, will undoubtedly improve our understanding of the functioning of arid and semi-arid ecosystems.

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